ORIENTATION AND BIORHYTHMS IN JUMPING SPIDERS (ARANEIDA: SALTICIDAE)

By

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INTRODUCTION

It has been known from time immemorial that living organisms show differences in behavior at different times of the day and at different seasons. The ancient Tamil Sangam literature, consisting of eight anthologies and ten idylls dating from the eighth century B. C. to the second century A. D., has numerous references to these. Translations of two extracts read as follows:

> The crow which is weaker than the owl can defeat the owl in the daytime but cannot do so at night.
>
> -Thirukural

> When the clouds are heavy with rain and it thunders, the blue-necked peacock spreads its beautiful tail and dances.
>
> -Nathinai

The work of Aristotle (384-322 B. C.) also refers to animal activities like the nocturnal eclosion of cicadas and the resting of fishes, bees, and other animals.

Orientation and Biorhythms in Animals

The earliest experimental study of diurnal rhythms is credited to the French astronomer, DeMairan (1729), who noted that the diurnal movements of certain plants persisted when they were kept in constant temperature and continuous darkness. Since then a large amount of information has been accumulated on the diurnal, lunar and seasonal activity rhythms of animals. The study of diurnal activities has attracted most attention. A detailed discussion of many problems connected with biological rhythms is found in the 1960 Cold Spring Harbor Symposium on

Quantitative Biology. The nature of the diurnal rhythm and its occurrence in nature has been discussed in numerous articles and reviews (for example: Bruce and Pittendrigh, 1957; Webb and Brown, 1959; Harker, 1961; and Bünning, 1964).

Time-compensated animal orientation is a related subject, which refers to the mechanism involved that aids in the response of the organism to environmental stimuli changing in the course of the day and the season. This field has been a topic of intense experimental work as judged, for example, by the reviews of Autrum (1963) and Sauer (1964).

Use of Spiders in Ethological Studies

Spiders have been used in a number of ethological investigations. Time-compensated sun orientation has been found in the Agelenidae and Lycosidae (Bartels, 1929; Görner, 1962; and Papi, 1955). The Theridiidae have been used for a study of the attributes of their webs (Wolcott, 1963). The Argiopidae were given the greatest attention in an attempt to analyze the complex behavioral patterns involved in web building (Barrows, 1915; Peters, 1953; and Bay, 1962), and also to study the effects of drugs on behavioral patterns (Witt and Reed, 1965).

The hunting behavior of salticid spiders, which do not use a web to trap their prey, is well suited for a study of internal motivation and drive levels, as it consists of a long chain of responses (Precht and Freytag, 1958; Drees, 1952; and Gardner, 1964). Courtship behavior and perceptual mechanisms have been the subject of intense studies by the Peckhams (1890), Bristowe (1929), Crane (1949), Heil (1936), Kaston (1936) and Dzimirski (1959).

Except for the laboratory observations on a single species by Branson and Hollis (1964), very little has been done on the subject of orientation and nothing on biorhythms in jumping spiders. It has been generalized that they are strictly diurnal (Crompton, 1950), and that they exhibit a simple type of menotactic orientation (Savory, 1964). In order to test the validity of these generalizations and to increase our understanding of the salticid spiders, the present study was undertaken.

MATERIALS AND METHODS

The Jumping Spiders

The jumping spiders are active during daytime, and some of them have a keen sight, being able to stalk prey from afar. They have elaborate courtship activities controlled by optical sign stimuli. Members of this family are recognized by their jumping habits, a short compact body, and a broad cephalothorax with four large eyes directed forward and four additional ones in two dorsal rows. The short strong legs bear ungual tufts. The jumping spiders do not spin elaborate webs, except for patches of silk tubes for their night retreats, hibernation, molting, and protection of their eggs.

Millot (1949) lists over 3,000 species in 474 genera, most of them found in the tropics. Comstock (1920) estimates 300 species in 40 genera living in America north of Mexico, and Richardson (1950) reports 46 species of 24 genera from northern Florida alone.

A preliminary survey of the salticid spiders of Gainesville was undertaken during the early part of the study. Three species most abundant and easily available throughout the year were used in the experiments. The three represent three separate subfamilies according to the classification of Petrunkevitch (1939), and Roewer (1954).

Subfamily:	Spider:
Marpissinae:	*Menemerus bivittatus* (DuFour), 1831.
Dendryphantinae:	*Phidippus regius* (Koch), 1846.
Plexippinae:	*Plexippus paykulli* (Audouin), 1827.

Menemerus bivittatus (DuFour), 1831

Male: 7 mm; Female: 9 mm (Fig. 1). This cosmopolitan species is abundant in the tropical and subtropical regions, and is best known through the works of DuFour (1831), Comstock (1920), Richardson (1950), and Barnes (1950). Its flattened body is cryptically colored, and it is well adapted for living under the bark of trees. The specimens used in the experiments were collected under the bark of pine and oak trees. These spiders feed on small insects such as mosquitoes and flies. They have been observed to line up in front of an ant trail and grab ant pupae transported in the jaws of worker ants. This is contrary to the remarks of earlier naturalists about the 'fear of ants' by spiders.

Apart from studying them in nature, ten adults were marked with red nail polish on the rear of the cephalothorax and released on June 25, 1965 in the field (Fig. 3e). They readily constructed a web on the first night. Seven of the individuals returned to the same web each night during the first four days of observation, and the other three did not return to the web constructed on the first night. They did not appear to disperse very far from day to day. After a lapse of ten days one individual was found to have travelled the greatest distance of 15 feet from the point of release. Specimens marked with luminous paint and observed at night in the laboratory were active at night, supporting the information gained from recordings (p. 29).

Phidippus regius (Koch), 1846

Male: 14 mm; Female: 15mm (Fig. 2). These large jumping spiders, originally described from Cuba and Santo Domingo, occur in the southern part of the United States as well. They are known through the works of Koch (1846) and Bryant (1943). They occur in a wide variety of habitats,

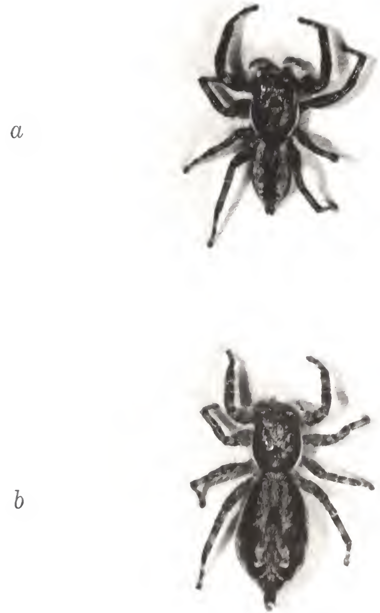


Fig. 1. *Menemerus bivittatus* (DuFour).
(a) Male: 7 mm, (b) female 9 mm,
(actual measurements).

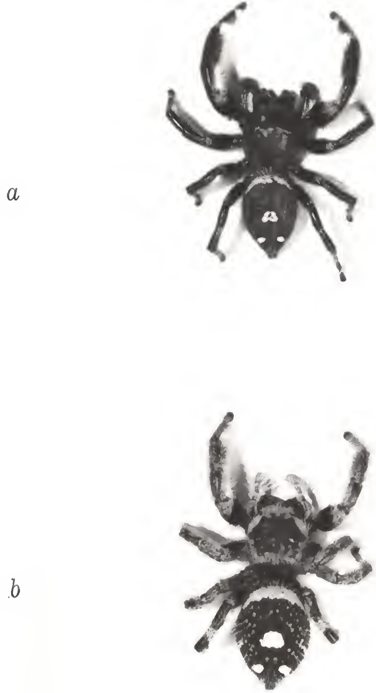


Fig. 2. Phidippus regius (Koch).
(a) Male: 14 mm, (b) female: 15 mm
(actual measurements).

for example in the turkey-oak forests and palmetto scrub. The individuals used in the experiment were collected on yucca plants (Yucca filamentosa). More than two spiders were rarely found on the same plant; the webs were always constructed on the upper surface of the leaf (Fig. 3c and d). The compass bearings of 24 webs built on yucca plants were taken on May 14, 1966 in Gainesville, along Highway 441 (Fig. 3a); an additional 22 webs were recorded on October 16, 1966 at Marineland, 70 miles east of Gainesville (Fig. 3b). The magnitudes of the mean vectors (east or west of the north-south line) for the two localities are as follows:

Gainesville: South-east, r=0.921; North-west, r=0.836.

Marineland: North-east, r=0.957; South-west, r=0.872.

These observations show a bimodal distribution in the construction of their webs on the plant (Fig. 4).

Plexippus paykulli (Audouin), 1827

Male: 10 mm; Female: 12mm (Fig. 5). This cosmopolitan species is common in the warmer regions of the world; it is known through the descriptions of Audouin (1827), Peckham and Peckham (1909), Dyal (1935), Richardson (1950), and Phanuel (1963). In Gainesville, they were collected from palmettos and fallen vegetation and on buildings and bridges (Fig. 3e). The adults built their webs at distances from one another and maintained their social distance even under crowded conditions. Measurements between webs in linear rows on bridges gave a mean distance of 15 inches with a standard deviation of four inches (n=20). No cannibalistic tendencies were noticed, although threat behavior was displayed between individuals when encounters were made near the web or during their hunting activities.

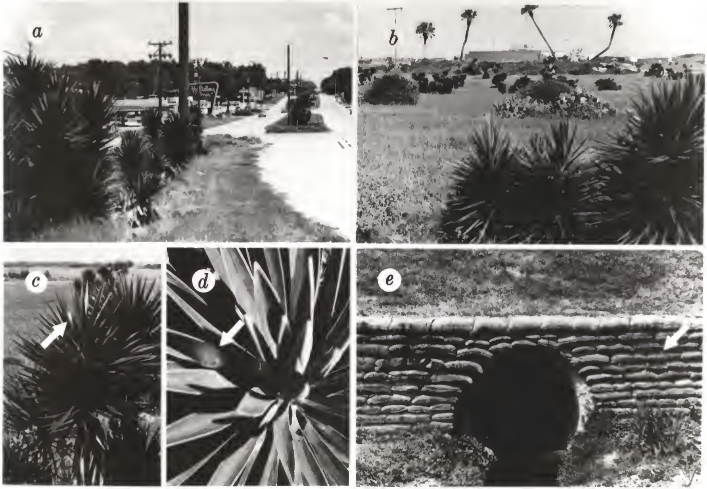


Fig. 3. Field-work localities, (a) Yucca plants planted north-south in Gainesville, (b) random growth at Marineland, (c) lateral and (d) top views of the web of Phidippus regius on yuccas. (e) Locality where the marked specimens of Menemerus bivittatus were studied; arrows indicate webs.

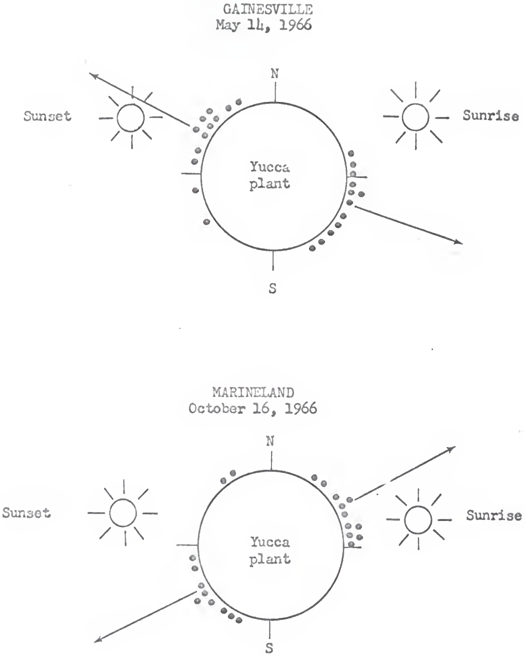


Fig. 4. Orientation of 46 webs of *Phidippus regius* on 46 different yucca plants.

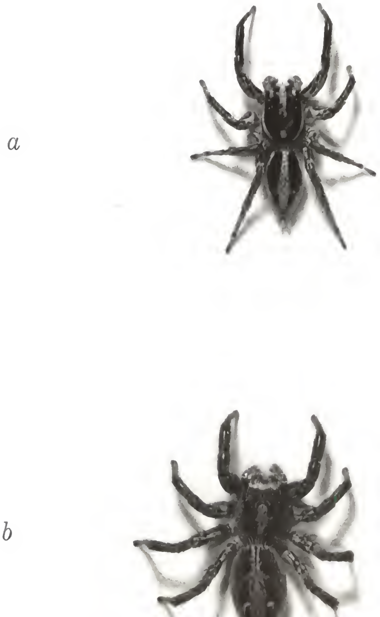


Fig. 5. Plexippus paykulli (Audouin).
(a) Male: 10 mm, (b) female:12 mm
(actual measurements).

Bi-weekly and monthly collection trips were made from 1964 to 1967. The ratio of adults to penultimates provides an index of their relative abundance (Fig. 6).

Recording of Daily Activity Cycles

Supplementing field observations, the spiders' activity cycles were studied in the laboratory.

Spiders that were brought into the laboratory were kept under light-dark cycles in phase with the local rhythm of day and night. The large *Phidippus regius* were kept in transparent boxes (22 x 6 x 7 cm) and fed with mealworms; the smaller forms were reared in vials and fed on *Drosophila*.

Preliminary field observations indicated that these spiders are continuously active for long periods of the day. The following experimental set was built. Wooden cages (10 x 25 cm) held glass tubes containing the spiders (Fig. 7a). The two walls of a cage had holes for holding the photocell and sensors of the Hunter photocell relay Model 335S. A 6.3 volt lamp was used with an infrared filter; when the spider broke the beam of light, the event was relayed to the Esterline Angus recorder (Model 6417-14). The chart drive was set at a speed of 3/4 inch per hour.

The spider with its holding cage was lodged in a constant temperature chamber (Fig. 8). A 40 watt day-light bulb inside the chamber was controlled by an automatic timer (Paragon Electronic Co. Model APT5.0); the humidity was determined with a relative humidity indicator (Honeywell Model W611A).

Two to four spiders were used at a time and allowed a period of 24 hours to adjust to the habitat before the recording began. Then the

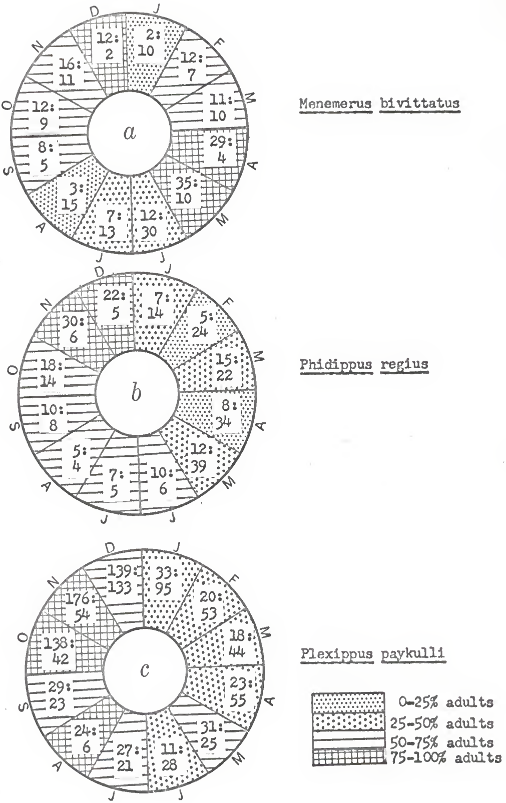


Fig. 6. Seasonal variation in proportion of adults and penultimates collected in Gainesville from January to December, 1964-1967. Figures represent number of adults: number of penultimates.

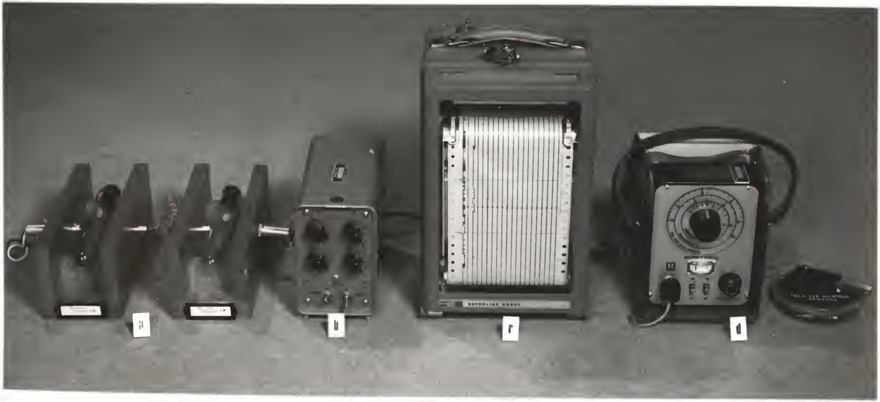
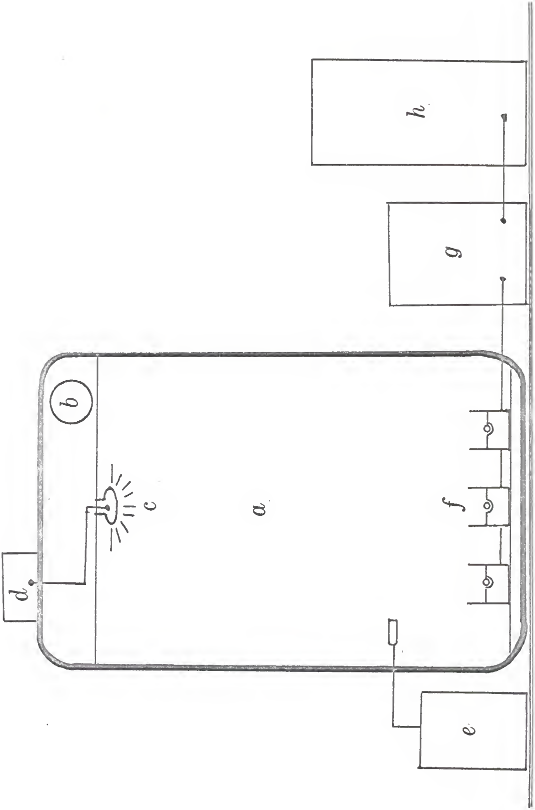


Fig. 7. Apparatus for the recording of daily activity cycles in jumping spiders. (a) Spiders in tubes with holding cages, (b) photocell relay , (c) Esterline Angus recorder, (d) relative humidity indicator.

Fig. 8. Experimental setup for the recording of locomotor activity. (a) Constant temperature chamber, (b) temperature dial, (c) light, (d) timer controlling light, (e) relative humidity indicator, (f) spiders in tubes with holding cages, (g) photocell relay, (h) Esterline Angus recorder.


d
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following categories of recordings were made: (a) six to 12 days at 25°C in 12 hour light and 12 hour dark cycle; (b) four to six days at 25°C in continuous darkness; (c) four to six days at 25°C in continuous light; (d) six days at 35°C in a 12 hour light and 12 hour dark cycle; and (e) phase-shift in a reverse rhythm of light-dark cycle for six days at 25°C. Only females were used, and they were not fed during the period of recording.

Orientation in the Field under the Clear Sky

Spiders were released in the center of a circular wooden disc, 60 centimeters in diameter. Faint pencil lines divided the surface into 16 equal sectors. The margin of the disc had a groove in which the spiders could hide after reaching it. The sector which each spider chose was noted; the spider was captured from the margin and released in the center for a total of ten trials in each of the following five experimental sessions:

1. Morning: 0600-0800 hrs.
2. Forenoon: 0900-1100 hrs.
3. Noon: 1130-1230 hrs.
4. Afternoon: 1500-1600 hrs.
5. Evening: 1800-1900 hrs.

The spiders were collected one to three days prior to the experiment, and they were kept in the laboratory under normal day-night and temperature conditions.

The spiders were always released singly in the following way. A spider was placed in the center of the disc and covered with a shallow black cup. One minute later, with a quick upward motion of the cup, the spider was released. The most common pattern of behavior was that the spider would turn once or twice and then advance in a particular direction. If a spider remained motionless for more than two minutes, or if it erratically jumped in various directions, it was counted as not showing orientation.

For the entire experiment the observer remained motionless in a position north of the disc. A lensatic compass was used to set the mid-point of one of the sectors of the disc directly facing north. The position of the disc was randomized by rotating it, and the surface was cleaned of silk threads between trials.

All of the experiments were conducted in the open playing fields of the University campus in Gainesville (29° 37'N, 82° 21'W). The temperature and relative humidity were noted at the time of the experiment with a sling psychromoter. Eastern Standard Time (EST) minus 29 minutes gave the Local Mean Time (LMT), and the azimuth position of the sun at this time was computed for Gainesville from the tables in the U. S. Naval Oceanographic Publication No. 260 (1964).

Ten adult females of each of the three species were tested at times when the wind speed was less than ten miles per hour and when the sky was clear (concerning cloud effects, see p. 53).

For the recording of the ten angular measurements (α_1 to α_{10}) made by each spider in each session, the mean angle (θ), and the length of the mean vector (r) were calculated after the methods suggested by Batschelet (1965). If α_1 to α_{10} are the angular measurements made from the north, the components of the resultant vectors X and Y are given by the expression:

$$X = \frac{1}{n} \sum_{i=1}^{n} \text{Cos}\, \alpha_i$$

$$Y = \frac{1}{n} \sum_{i=1}^{n} \text{Cos}\, \alpha_i$$

The values Y/X and X/Y gave the values of $\tan\alpha$ and $\cot\alpha$, with which the mean angle was computed from the table of natural trigonometric functions for angles (Selby and Girling, 1965). The length of the mean vector (r) is given by the expression:

$$r = \sqrt{X^2 + Y^2}$$

Since the group interval was large in this experiment, each of the 16 sectors including 11.25°, a correction analogous to the Shephard correction was necessary (Batschelet, 1965). The calculated (r) X 1.0067 gave the corrected value of (r). The measure of dispersion (s) was calculated for each case and is given by the expression:

$$S = 2\sqrt{(1-r)}, \text{ in radians.}$$

Radians were converted to degrees, using the table of Fisher and Yates (1957). Rayleigh test for randomness was applied to each case using the formula: $z = nr^2$.

Orientation under a Fixed Light Source

In order to test the orientation of the spiders to a fixed light source, a 150 watt floodlight was fixed at an angle of 60 degrees at a distance of eight feet from the center of the orientation disc, north of it, and opposite the mid-point of one of the sectors. Two adult females of each of the three species were tested at two-hour intervals for a period of 24 hours. The spiders were kept under a light-dark cycle which was the same as that of the natural cycle before and during the days of the experiments.

The experiment was conducted in a darkroom. It was started at 0600 EST on March 14, 1967, and ended at 0400 EST the following day. The temperature in the room ranged from 70 to 80°F, and the range in relative humidity was 60 to 68 percent. The observations were made from behind the light source. As in the previous experiment, each spider was released singly and given ten trials during each experimental session.

Experimental Shift and Resetting of the Internal Clock

The method of an experimental phase-shift of the internal clock of an animal is used to test its capabilities for sun orientation. The organism is first subjected to a light-dark cycle out of phase with the natural day-night rhythms to which the animal has been exposed. When the animal has reached a new steady-state of activity and rest under the influence of the new cycle, its orientational response is then tested under the natural sun. If the experimental day begins six hours later than the local day, the experimental animals are expected to shift their preferred direction of orientation about 90 degrees to the right of their original choice before the time-shift, provided they are utilizing a sun compass orientation based on the azimuth position of the sun alone. With this method sun compass orientation has been confirmed for many animals (examples are given by Papi, 1955; Birukow, 1960; Braemer, 1960; and Hoffmann, 1960).

All three species of spiders were used in this experiment. Their internal clock was shifted six hours in advance of the natural dark-light cycle. The spiders were kept in a constant temperature chamber set at 25°C, and exposed to a relative humidity range of 70 to 75 percent. Eight females of Plexippus paykulli were treated in the chamber for six days and then tested for orientation under the sun. Eight spiders of the same species at the same locality served as control. Ten trials were performed with each spider under the clear sky (for method, see p. 17). The experiment was repeated with eight (four control and four experimental) spiders of each of the other two species, Menemerus bivittatus and Phidippus regius.

The mean angle (θ) and the length of the mean vector (r) were calculated for each group of spiders using the formula given by Batschelet (1965). To test whether the orientation of the experimentals is in any way different from the control animals, the parametric two-sample test of Watson and Williams (1956) was used. This is given by the expression:

$$F = (N - 2)\,\frac{R_1 + R_2 - R}{N - R_1 - R_2}\quad\text{, where}$$

N = the combined value of the two samples n_1 and n_2,

R_1 and R_2 = the length of the mean vectors of the respective samples ($r \times n$)

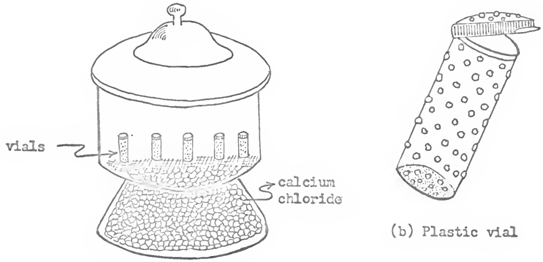
R = the resultant vector of the combined samples, and

F, has the form of a variance ratio; the calculated value to be compared with the 'F' value for 1 and N-2 d. f. in the tables of Fisher and Yates (1957).

The Effect of Desiccation on the Light Reaction of Plexippus paykulli

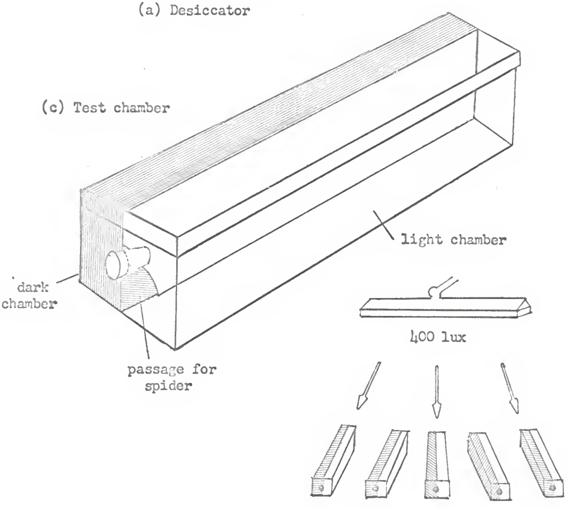
An animal can be said to be desiccated when it is in a relatively inactive dry state due to complete or nearly complete deprivation of moisture. This can occur in nature under abnormally dry conditions. In the present study, the effect of desiccation on the behavior of Plexippus paykulli in reaction to light has been investigated.

The spiders were collected one to two days prior to the experiment. Mature males and females were tested five at a time, in perforated plastic vials placed in a desiccator with anhydrous calcium chloride (Fig. 9a). The desiccant gave a relative humidity value of 10 to 15 percent inside the jar desiccator. A Honeywell-W611A Portable relative humidity indicator was used to determine the relative humidity. The



(b) Plastic vial

(a) Desiccator



(c) Test chamber

(d) Experimental set up

Fig. 9. Apparatus used in the experiments on the effect of desiccation on the light reaction of Plexippus paykulli.

experiment was in constant temperature at 37°C, in a cycle of 12 hours light and 12 hours dark.

After varying lengths of desiccation, the spiders were transferred to the 'dark-light alternative chamber' (Fig. 9c) to test their light response. The test chamber consisted of a plastic box (22 x 6 x 7 cm), in which an opaque partition was inserted in the mid-sagittal plane, and one half of the box was painted black. A hole of one centimeter in diameter, closed by a stopper, was made on one side at the junction of the partition to release the spider into the chamber. Five chambers were used at a time and were exposed to a uniform illumination of 400 lux from a lamp two meters above the set.

The position occupied by each of the five spiders was noted at one-minute intervals for a period of ten minutes. They were scored 'L' or 'D', depending on the side of the chamber they occupied. The total score for the batch of five spiders was calculated for each experiment. The intensity of light reaction was calculated for the batch of five, and expressed as the excess percentage on the illuminated side of the chamber. The formula of Perttunen (1963) was used in the calculations:

$$\text{Excess percentage on the illuminated side} = \frac{100\,(L - D)}{N}\text{, where}$$

L = number of positions recorded on the light side of the chamber,

D = number of records on the dark side of the chamber, and

N = the total number of positions recorded, including the small number occupying the narrow middle line (N=50, in all the experiments).

All the experiments were performed during the afternoon, 1400 EST to 1700 EST (in the month of November, 1965). The temperature in the room ranged from 25 to 29°C with a relative humidity range of 35 to 40 percent. Different individuals were used for each experiment, including the ones 'before desiccation.' The individuals tested 'before desiccation' also served the function of a 'control' for purposes of comparison.

Oxygen Consumption and Acid Phosphatase Activity

A physiological test was conducted that has a bearing on the daily activity cycles of the jumping spiders. A determination of oxygen consumed by the spider at different times of the day was made.

The rate of oxygen consumption is commonly taken as an indicator of the metabolic state of an animal. To investigate this, adult females of the three species, two each of *Menemerus bivittatus* and *Phidippus regius* and five of *Plexippus paykulli*, were tested in a Gilson differential respirometer, following the method of Umbreit, Burris and Stauffer (1964).

The females were kept under the normal dark-light conditions for a few days and were weighed with an analytical balance before the start of the experiment at 1800 EST on July 2, 1966. The temperature of the water-bath was maintained at 25°C. During the twelve hours of the night the apparatus was covered with a black canvas which was removed in the morning. Thus the spiders were exposed to a 12 hour light and 12 hour dark condition during the 24 hour period of the experiment. Their oxygen consumption was measured for twenty-minutes' duration every hour for the continuous period of 24 hours.*

During the month of November, 1965, when *Plexippus paykulli* were collected in large numbers, the differences in the level of enzyme, in this case acid phosphatase, were tested with adults of the two sexes, and between adults and penultimate stages of each sex. The spiders were sorted out in four categories according to external morphological characters (Fig. 10).

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*Experiment conducted in collaboration with J. A. Anderson of the Department of Zoology, University of Florida.

Phosphatases are groups of enzymes in animal tissues that act on a variety of phosphate esters. They are broadly classified into acid and alkaline phosphatases, based on their affinity to specific types of ester linkages and the optimum pH necessary for activity. Acid phosphatases act optimally on monoesters of phosphoric acid at pH values near five.

A preliminary investigation with four different acetate buffers (of pH values 4.8, 5.0, 5.3, and 5.6) revealed a pH of 5.3 as the optimum for study of this enzyme in Plexippus paykulli. The tests were made at the same time of the day, between 1500 to 1700 EST. The spiders were weighed in separate vials correct to 0.0001 grams with an Ainsworth chain-weight balance. Ten to 16 individuals were used in each determination. They were anesthetized with CO_2; a homogenate was prepared by grinding spiders in a mortar with sand, using as a base 5 to 6 ml of distilled water at zero degree centigrade. The homogenate was centrifuged and kept at zero degree centigrade.

The substrate used was P-nitrophenol phosphate which reacted with the phosphatases in the spider homogenate, producing P-nitrophenol and phosphoric acid. The P-nitrophenol turns yellow in an alkaline solution. The amount of P-nitrophenol was determined with a spectrophotometer (Beckman DB) at 415 mμ and compared with a standard curve for P-nitrophenol. From this value the amount of P-nitrophenol produced per mg spider tissue was calculated. For each determination an assay tube contained the

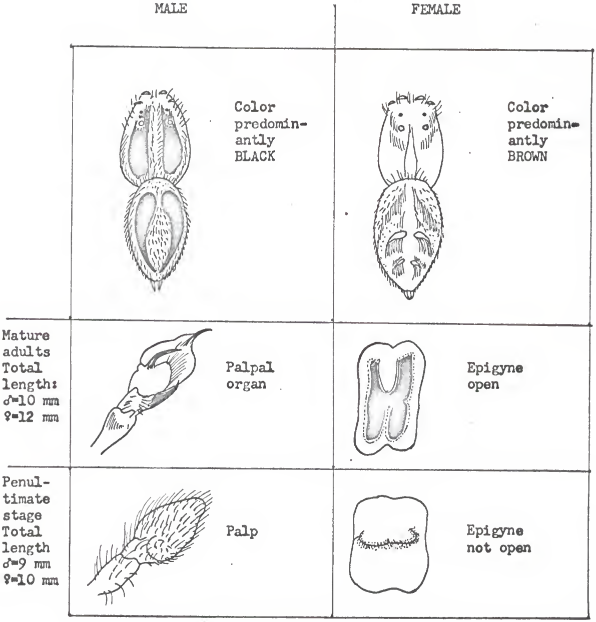
MALE
FEMALE
Color predominantly BLACK
Color predominantly BROWN
Mature adults Total length: ♂=10 mm ♀=12 mm
Palpal organ
Epigyne open
Penultimate stage Total length ♂=9 mm ♀=10 mm
Palp
Epigyne not open

Fig. 10. Identification of the sex and age of Plexippus paykulli.

following:

2 ml of 0.1 molar citrate buffer at pH 5.3
1 ml of distilled water
1 ml of substrate (0.025 M disodium P-nitrophenol phosphate)
1 ml of enzyme extract from spider.

One tube was used as a control, with an additional ml of distilled water instead of the enzyme. Each tube was agitated for quick mixing, and one ml was pipetted into a tube containing 10 percent potassium carbonate. This became the zero time sample. The remaining 4 ml in each tube were incubated at 37.5°C for 60 minutes in a water-bath; then 1 ml was added to 10 ml of potassium carbonate. The latter arrested enzymatic activity and facilitated spectrophotometric reading at the required wave length by turning the end product of the reaction yellow. The absorbance at 415mμ of both zero time sample and one-hour incubated samples were immediately determined in a spectrophotometer. Each value in Table 6 (p. 63) is the mean of four determinations from each homogenate. A total of four separate homogenates was made for each of the four categories of spiders.*

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*Experiment conducted in collaboration with F. Killingsworth of the Department of Entomology, University of Florida.

RESULTS

Recording of Daily Activity Cycles

For a comparison of the activity patterns of the different species, the various recordings of locomotor activities were grouped and the diurnal and nocturnal activities under the given experimental conditions were compared and analyzed (Figs. 11-17).

These experiments in general confirm the results of the field observations and in addition reveal certain aspects of the spiders' biorhythms which were not observed in nature. The recordings in the 12 hour light and 12 hour dark rhythms showed some activity during the night; the extent varied with the species. For Menemerus bivittatus the nocturnal activity was 19 percent of the diurnal activity, and the corresponding values for Phidippus regius and Plexippus paykulli were 29 and 4 percent respectively (Fig. 13). It is also noticed that as the day activity decreased, the night activity increased in the two species Menemerus bivittatus and Phidippus regius (Fig. 14 a, b).

Phidippus regius and Plexippus paykulli were not only active during the day for longer periods of time (Figs. 11b, 12), but were relatively more active per unit of time than Menemerus bivittatus (Fig. 13).

Field observations have shown that the three species have two peaks of activity during daytime. Menemerus bivittatus shows the peaks of activity between 0900 - 1000 and 1500 - 1800 EST, Phidippus regius during 0900 - 1000 and 1400 - 1700 EST, and Plexippus paykulli from

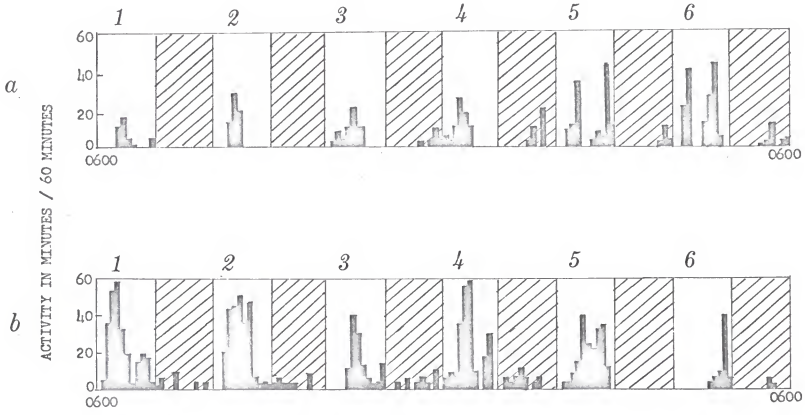


Fig. 11. Activity for six continuous days in periods of 12 hour light (clear), and 12 hour dark (striped) at 25°C. (a) Menemerus bivittatus No. 2., from December 25, 1966, (b) Phidippus regius No. 6., from February 3, 1966 onward.

Fig. 12. Activity of *Plexippus paykulli* No.4., for 12 continuous days in a 12 hour light (clear), and 12 hour dark (striped) period at 25°C from March 6, 1966 onward.

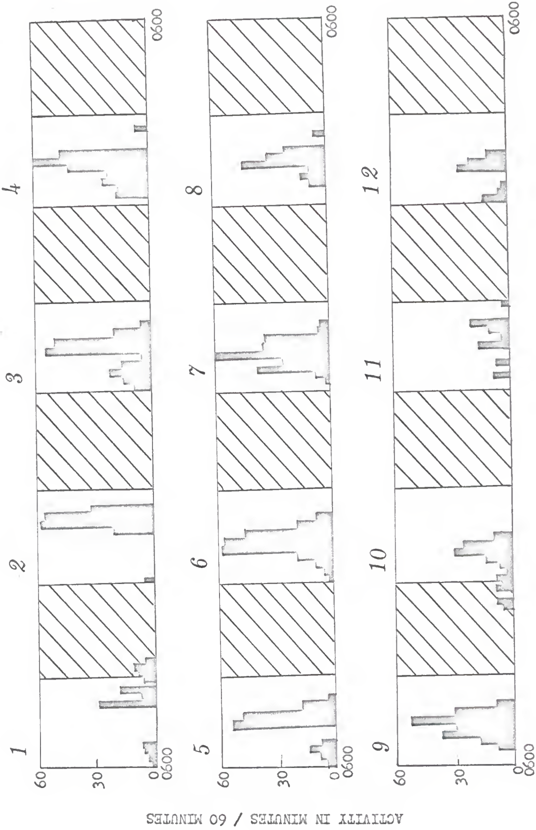

1
2
3
4
5
6
7
8
9
10
11
12
60
30
0
0600
0600
ACTIVITY IN MINUTES / 60 MINUTES

Fig. 13. Summaries of the activity cycles during the first six days at 25°C. (a) Menemerus bivittatus, mean value from recordings of three spiders; (b) Phidippus regius, eight spiders, (c) Plexippus paykulli, eight spiders.

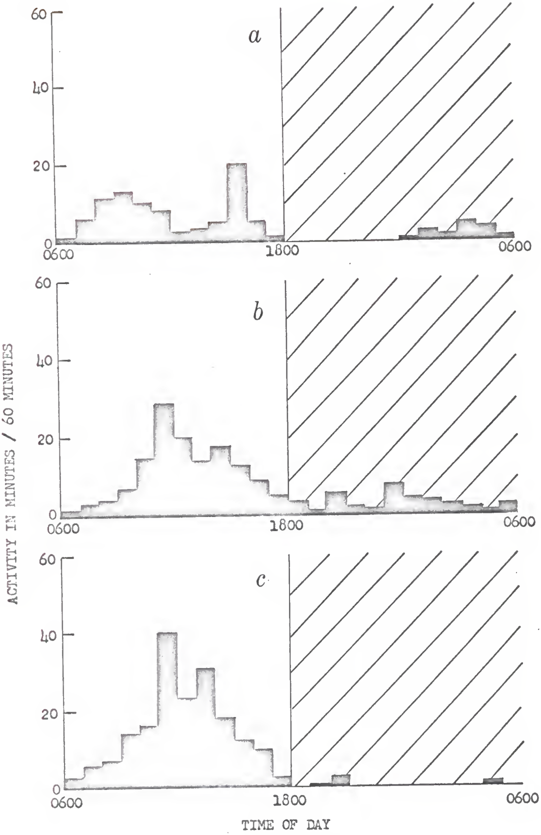
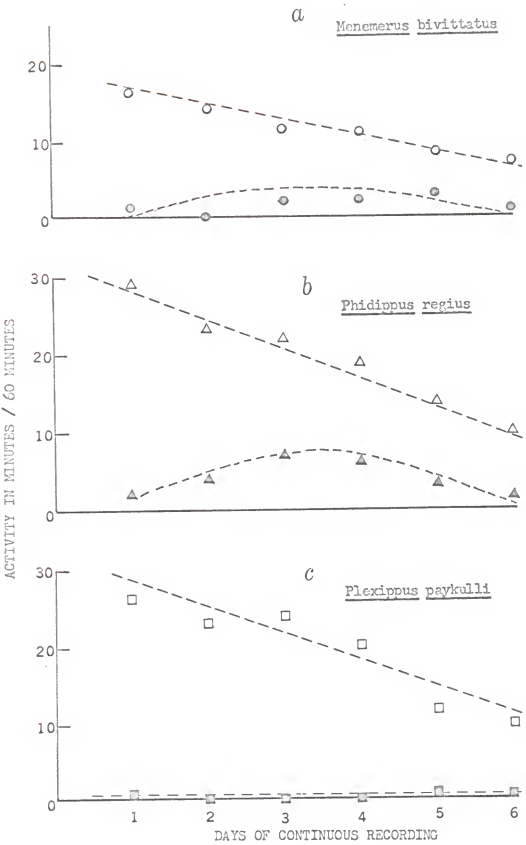

a
b
c
60
40
20
0
0600
1800
0600
ACTIVITY IN MINUTES / 60 MINUTES
TIME OF DAY

Fig. 14. Diurnal and nocturnal activities of (a) *Menemerus bivittatus*, (b) *Phidippus regius*, and (c) *Plexippus paykulli*. Mean activities per hour of the 12 hour light periods (○ △ □) and dark periods (● ▲ ■).


a
Menemerus bivittatus
20
10
0
b
Phidippus regius
30
20
10
0
c
Plexippus paykulli
30
20
10
0
ACTIVITY IN MINUTES / 60 MINUTES
1
2
3
4
5
6
DAYS OF CONTINUOUS RECORDING

0900 - 1000 and 1400 - 1800 EST at Gainesville. The recordings of their activities in the laboratory confirm these findings, although the two peaks tend to merge, especially in the latter two species, and when data for each species are pooled (Fig. 13).

Recordings in continuous light and continuous darkness revealed a free running rhythm, and indicated that light is an important entraining agent ('Zeitgeber'). Continuous darkness lengthened the peak of activity in *Plexippus paykulli* during the first four days (Fig. 15c). Then the spiders became less active, built a web, and finally remained inactive. The activity patterns of *Menemerus bivittatus* and *Phidippus regius* in continuous darkness remained about constant; however their peaks of activity became delayed from day to day, indicating an advancing shift of the period (Fig. 15). Also in these species the activity ceased after four days in continuous darkness.

Continuous light made *Phidippus regius* continuously active, with an indication of peaks appearing at increasing intervals of more than 24 hours (Fig. 16b). After the sixth day the activity of *Phidippus regius* faded, and the spiders became inactive. The other two species showed a pattern of activity similar to that in continuous darkness (Figs. 15 and 16), and after the fourth day they too showed a sharp decrease in activity. Once a web was fully built, the spiders remained inactive. A difference in temperature of ten degrees centigrade did not produce a change in the pattern or degree of locomotor activity in *Plexippus paykulli* (Figs. 12 and 17a).

The peak of locomotor activity was shifted by reversing the light-dark cycle for *Plexippus paykulli*. When the light-dark cycle was reversed (Fig. 17b), the onset of the first phase of activity and its

Fig. 15. Activity in continuous darkness for 96 hours, (a) *Menemerus bivittatus* No. 6., from November 18, 1966, (b) *Phidippus regius* No. 11., from November 1, 1966, (c) *Plexippus paykulli* No.9., from April 3, 1966 onward.

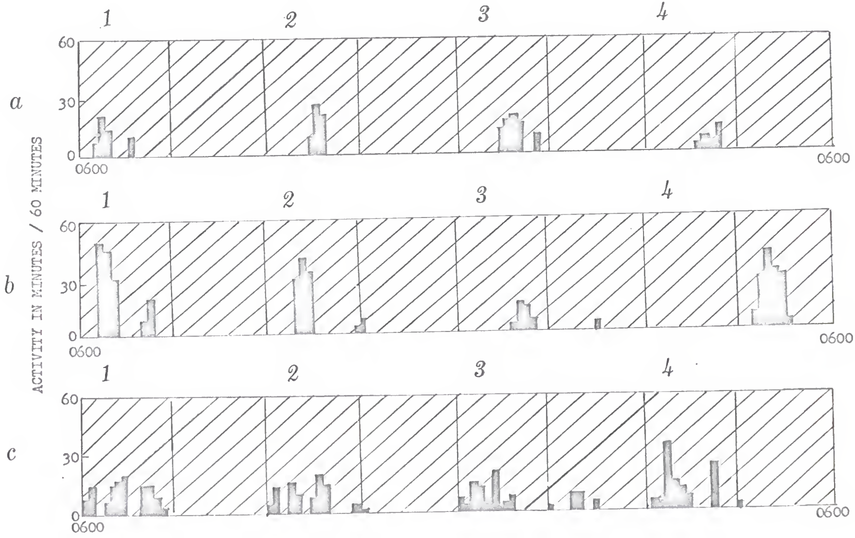
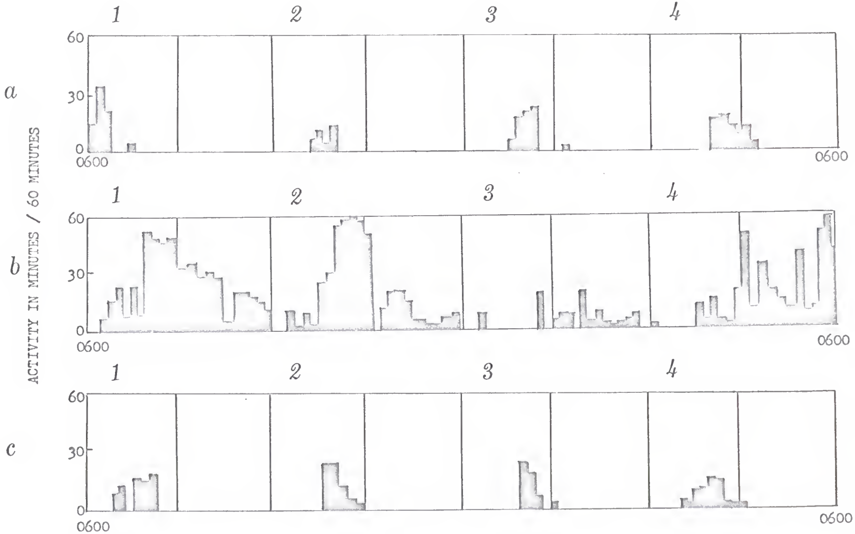

ACTIVITY IN MINUTES / 60 MINUTES
a
b
c
1
2
3
4
60
30
0
0600
0600

Fig. 16. Activity in continuous light for 96 hours. (a) *Menemerus bivittatus* No. 7., from September 26, 1966, (b) *Phidippus regius* No. 9., from September 21, 1966, (c) *Plexippus paykulli* No. 10., from April 11, 1966 onward.


1
2
3
4
a
b
c
ACTIVITY IN MINUTES / 60 MINUTES
60
30
0
0600
0600

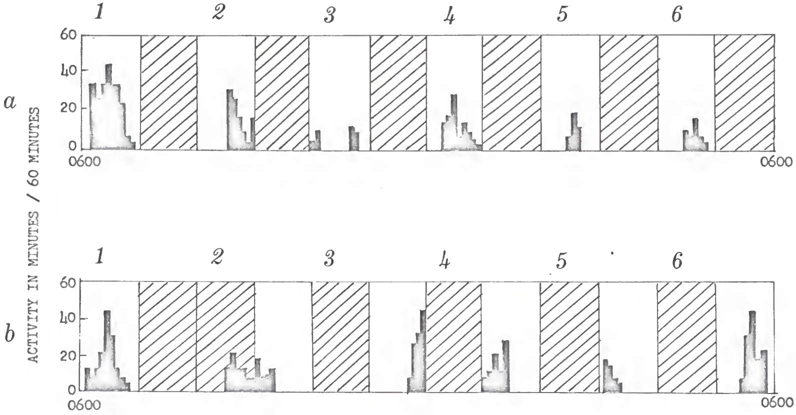


Fig. 17. Activity of *Plexippus paykulli* No. 11., in the normal dark-light cycle at 35°C, from November 10, 1966 onward, (b) recordings with the normal dark-light cycle reversed after the first day; *Plexippus paykulli* No. 13., from November 20, 1966 onward at 25°C.

peaks, now falling into the dark, were six hours delayed; this active phase was then terminated in daylight, two hours earlier than expected according to the original schedule. The next phase of activity occurred in the latter part of the second day of the new cycle, and from then on the spider's activity appeared synchronized with the new conditions. Thus the spider needed three days to adjust to the new rhythm. In the above experiments, the results of one individual alone are shown (Figs. 15 to 17), although recordings were obtained with two individuals of each species for each category studied; little variation was noticed between the two recordings of each species.

Orientation in the Field under the Clear Sky

The length of the mean vector (r), the mean angle in degrees (θ), and the probability value (z) applying the Rayleigh test for randomness are given in Tables 1 to 3.

For an understanding of the pattern of orientation of the individuals of each of the three species at the five periods of the day, together with the mean azimuth position of the sun at the time of the experiment, polar-wedge diagrams are shown (Figs. 19 to 21).

The experiments indicate the following:

(1) The spiders of the three species show definite patterns of orientation at different times of the day, although the magnitudes of the mean vectors are very weak.

(2) Most of the spiders are better oriented in the morning, forenoon, afternoon, or evening, and they are disoriented to varying degrees about noon.

(3) From the mean values of ($\bar{r}$), ($\bar{s}$), and ($\bar{z}$), plotted against the time of the day (Fig. 18), the following specific differences were found:

   (a) Menemerus bivittatus shows the least spread ($\bar{s}$) during the forenoon. In the field these spiders are most active at the same time, but do not begin their activities before the forenoon.

TABLE 1. Orientation of Menemerus bivittatus in the field under the clear sky.

# of	Morning			Forenoon			Noon			Afternoon			Evening		
Spider	(r)	(θ)	(z)	(r)	(θ)	(z)	(r)	(θ)	(z)	(r)	(θ)	(z)	(r)	(θ)	(z)
A1.1	.929	316	8.63**	.834	305	6.95**	.724	103	5.24**	.926	47	8.57	.956	225	9.14**
A1.2	.375	163	1.41NS	.885	176	7.83**	.664	163	4.41**	.910	261	8.28**	.895	58	8.10**
A2.1	.568	16	3.23*	.963	29	9.27**	.702	22	4.93**	.586	129	3.43*	.826	341	6.82**
A2.2	.925	20	8.56**	.942	88	8.87**	.784	65	6.15**	.938	233	8.80**	.939	193	8.82**
A3.1	.828	91	6.86**	.939	14	8.82**	.542	343	2.94*	.899	182	8.08**	.820	114	6.72**
A3.2	.953	194	9.08**	.681	230	4.64**	.589	281	3.47*	.940	283	8.84**	.709	308	5.03**
A4.1	.666	99	4.43**	.828	295	6.85**	.684	356	4.68**	.551	83	3.04*	.899	223	8.08**
A4.2	.423	357	1.79NS	.686	220	4.71**	.872	358	7.60**	.885	43	7.83**	.724	109	5.23**
A5.1	.628	111	3.94*	.901	218	8.12**	.826	226	6.82**	.523	198	2.73NS	.703	4	4.94**
A6.1	.879	234	7.73**	.948	240	8.99**	.275	284	0.76NS	.592	90	3.52*	.935	113	8.74**

(r) = Length of the mean vector; (θ) = mean angle in degrees; (z) = Value of Rayleigh test for randomness; *P < 5%, **P < 1%, NS = not significant.

TABLE 2. Orientation of *Phidippus regius* in the field under the clear sky.

# of	Morning			Forenoon			Noon			Afternoon			Evening		
Spider	(r)	(θ)	(z)	(r)	(θ)	(z)	(r)	(θ)	(z)	(r)	(θ)	(z)	(r)	(θ)	(z)
B1.1	.974	207	9.48**	.785	180	6.16**	.573	11	3.28*	.836	236	6.98**	.750	122	5.62**
B1.2	.945	230	8.93**	.881	5	7.76**	.495	299	2.45NS	.970	229	9.41**	.917	214	8.41**
B1.3	.916	4	8.39**	.948	345	8.98**	.276	255	0.76NS	.924	165	8.53**	.925	236	8.55**
B3.1	.872	223	7.60**	.815	224	6.64**	.715	22	5.11**	.230	129	0.53NS	.915	90	8.37**
B3.2	.848	182	7.19**	.627	42	3.93*	.096	242	0.09NS	.785	183	6.16**	.945	111	8.90**
B3.3	.886	154	7.84**	.850	337	7.22**	.887	282	7.86**	.651	105	4.23*	.656	98	4.30*
B3.4	.955	104	9.12**	.910	35	8.28**	.660	196	4.35**	.899	156	8.08*	.902	108	8.13**
B3.5	.806	35	6.49**	.833	337	6.93**	.599	317	3.58*	.760	109	5.77	.888	52	7.88**
B3.6	.820	112	6.72**	.940	167	8.83**	.480	96	2.30NS	.841	157	7.07**	.748	297	5.59**
B3.7	.958	133	9.17**	.766	96	5.86**	.734	343	5.38**	.957	225	9.15**	.933	209	8.70**

(r) = Length of the mean vector; (θ) = mean angle in degrees; (z) = Value of Rayleigh test for randomness; *P < 5%, **P < 1%, NS = not significant.

TABLE 3. Orientation of Plexippus paykulli in the field under the clear sky.

# of Spider	Morning (r)	Morning (θ)	Morning (z)	Forenoon (r)	Forenoon (θ)	Forenoon (z)	Noon (r)	Noon (θ)	Noon (z)	Afternoon (r)	Afternoon (θ)	Afternoon (z)	Evening (r)	Evening (θ)	Evening (z)
C1.1	.824	186	6.78**	.809	20	6.54**	.957	200	9.15**	.648	223	4.19*	.919	30	8.44**
C2.1	.960	259	9.21**	.867	264	7.51**	.202	192	0.41NS	.912	292	8.31**	.847	338	7.17**
C3.1	.967	144	9.35**	.920	332	8.46**	.578	148	3.34*	.902	34	8.13**	.945	72	8.73**
C4.1	.797	355	6.35**	.844	49	7.12**	.846	327	7.15**	.686	45	4.70**	.946	350	8.94**
C4.2	.861	349	7.41**	.930	185	8.64**	.673	298	4.52**	.839	357	7.03**	.684	359	4.67**
C5.1	.691	5	4.77**	.806	227	6.49**	.830	54	6.88**	.232	123	0.5NS	.914	9	8.35**
C5.2	.827	297	6.83**	.945	319	8.93**	.755	95	5.70**	.787	91	6.19**	.638	18	4.07*
C6.1	.436	51	1.90NS	.946	237	8.94**	.813	116	6.61**	.747	113	5.58**	.794	184	6.30**
C6.2	.764	125	5.83**	.783	239	6.13**	.559	61	3.12*	.517	121	2.67NS	.874	28	7.63**
C7.1	.826	300	6.82**	.806	12	6.49**	.467	37	2.18NS	.731	306	5.34**	.832	10	6.92**

(r) = Length of the mean vector; (θ) = mean angle in degrees; (z) = Value of Rayleigh test for randomness; *P < 5%, **P < 1%, NS = not significant.

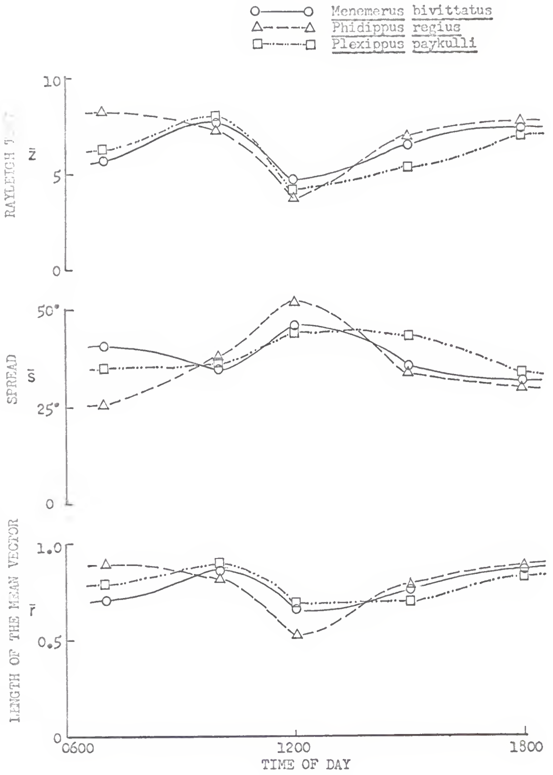
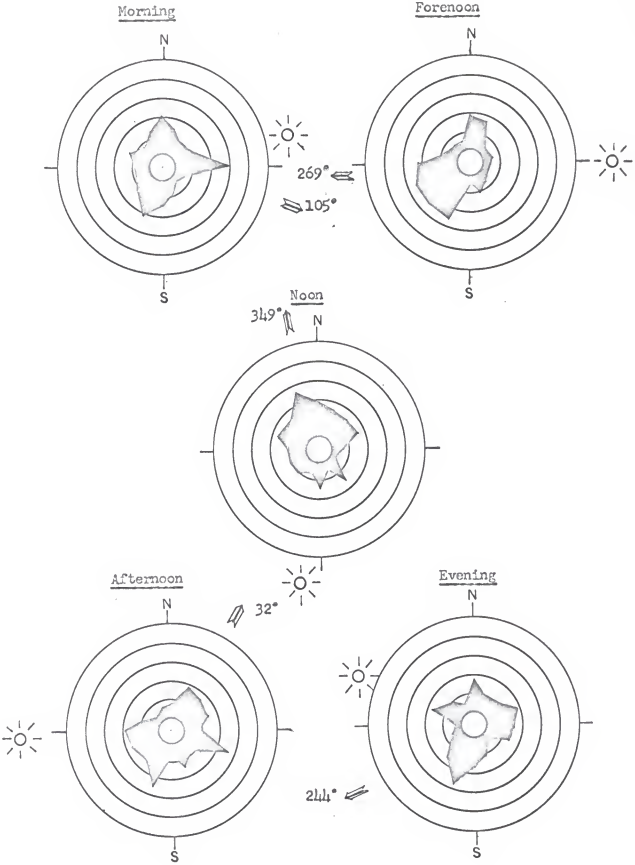


Fig. 18. Mean values of the length of the mean vector ($\bar{r}$), spread ($\bar{s}$), and the value of Rayleigh test for randomness ($\bar{z}$) of the three species of spiders at different times of the day.

Fig. 19. Orientation of *Menemerus bivittatus* under the clear sky.
(n = 100, mean angle = ⇒).


Morning

Forenoon

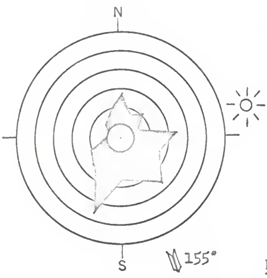
Noon

Afternoon

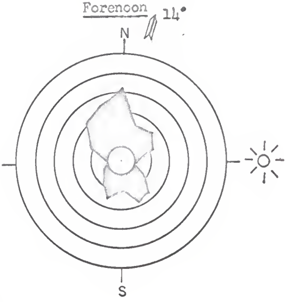
Evening

Fig. 20. Orientation of *Phidippus regius* under the clear sky.
(n = 100, mean angle =⇨).

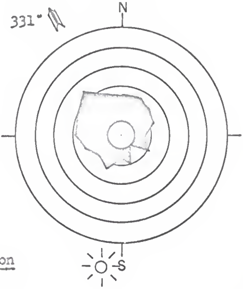
Morning



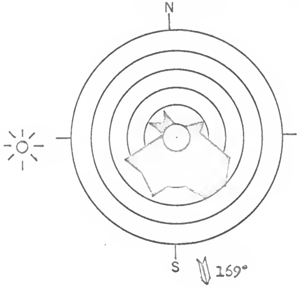
Forenoon



Noon



Afternoon



Evening

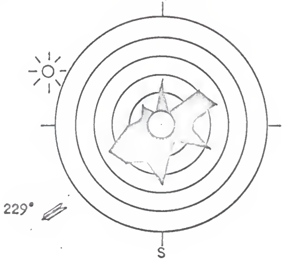
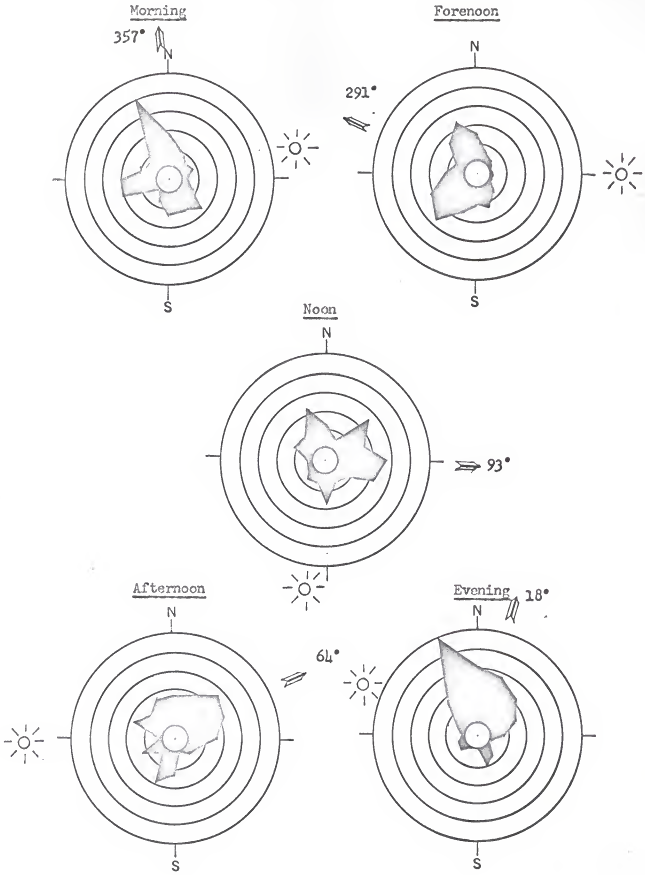


Fig. 21. Orientation of *Plexippus paykulli* under the clear sky. (n = 100, mean angle = ⇨).


Morning
357°
N
S
Forenoon
N
291°
S
Noon
N
93°
Afternoon
N
64°
S
Evening
18°
N
S

(b) *Phidippus regius* shows the greatest spread ($\bar{s}$)at noon compared to the other two species. Further, the spread at noon is almost twice that at the other times of the day.

(c) *Plexippus paykulli* shows the best overall orientation; the fluctuations in spread ($\bar{s}$) are the minimum for the three species at the different times of the day.

(4) The mean azimuth angle calculated for the ten individuals of *Plexippus paykulli* is plotted against the normal course of the sun (Fig. 22). This shows (a) that these spiders cross the path of the sun at about midday, and (b) that they keep the sun to one side before noon and shift to the opposite side of the sun after noon. *Menemerus bivittatus* keeps the sun to the left during the morning and forenoon, and it maintains the sun on its right after noontime (Fig. 19). *Phidippus regius* keeps the sun on its left in the morning and reverses its position in relation to the sun in the evening (Fig. 20). *Plexippus paykulli* shows the opposite tendency of keeping the sun to the right during most of the day and reversing its position in relation to the sun only in the evening (Figs. 21 and 22).

Apart from the above experiments, the following observations were made. When spiders were tested under heavy cloud cover they were found to be disoriented to varying degrees. They showed an orientation more consistent in direction, however, when tested a few minutes before sunrise or after sunset under the clear sky.

Orientation under a Fixed Light Source

Judged by the high values of (r) and low values of (s), the six spiders showed a strong orientation (Fig. 23). The mean values of the length of the mean vector ($\bar{r}$), spread ($\bar{s}$) and mean angles ($\bar{\theta}$) for each of the three species (2 individuals; 10 trials each for each of the 12 sessions) are as follows:

Menemerus bivittatus $\bar{r} = 0.896$, $\bar{s} = 25^\circ$, $\bar{\theta} = 69^\circ \pm 32$

Phidippus regius $\bar{r} = 0.914$, $\bar{s} = 23^\circ$, $\bar{\theta} = 85^\circ \pm 30$

Plexippus paykulli $\bar{r} = 0.891$, $\bar{s} = 26^\circ$, $\bar{\theta} = 70^\circ \pm 41$

The experiments also indicate that these jumping spiders tend

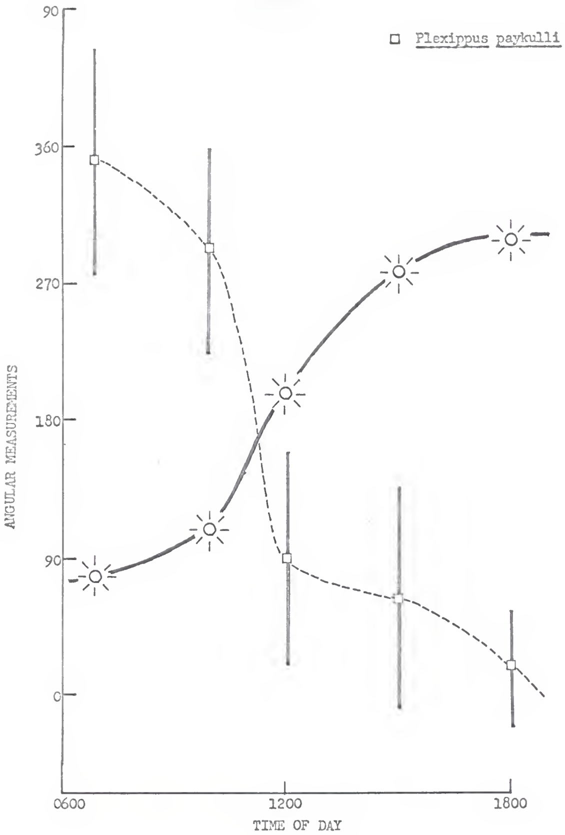


Fig. 22. Mean angle of orientation of Plexippus paykulli. Bars indicate spread (s) on either side of the mean; path of sun shown.

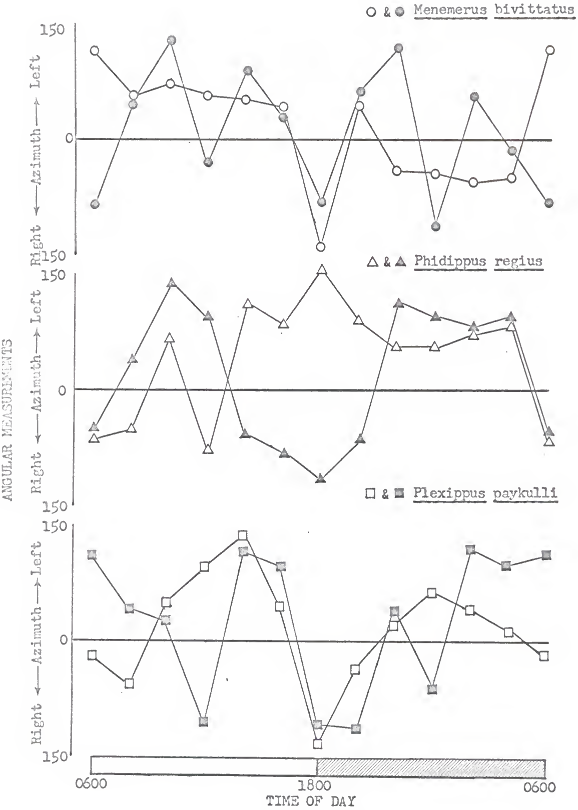


Fig. 23. Orientation of six spiders under a light source fixed at 60°.

to keep the light source to one side during one part of the day, and to shift to the opposite side later Under the experimental conditions a better estimate of the menotactic angle was obtained than under field conditions.

These results seen together with those obtained from the earlier experiments (p. 42) indicate that the sun orientation of these spiders is essentially menotactic as they tend to keep the sun to one side or the other during the course of the day.

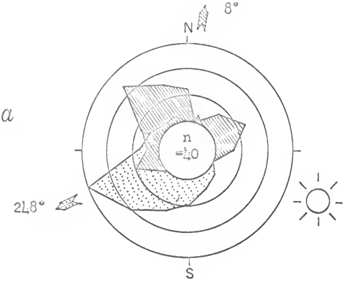
Experimental Shift and Resetting of the Internal Clock

A comparison of the orientation of control and experimental animals gave the 'F' value. For Plexippus paykulli this was calculated to be 5.63 which is greater than 'F' with 1 and N-2 d.f.=4.60; hence it is significant at 0.05 level. The calculated 'F' values for Menemerus bivittatus and Phidippus regius were 5.61 and 2.48 respectively, both not significant.

The results indicate that a phase-shift has varying effects on the different species. In Plexippus paykulli the two directions indicated by the control and experimental animals are significantly different, but the shift is about 92 degrees to the right rather than, as expected, to the left of the original direction. Phidippus regius shifts in the expected direction, although the two directions indicated are not significantly different while the time-shift corresponded to an angular shift of 131°. Menemerus bivittatus indicated a shift in the unexpected direction, and the two directions are not significantly different, although the angular shift is 120° (Fig. 24).

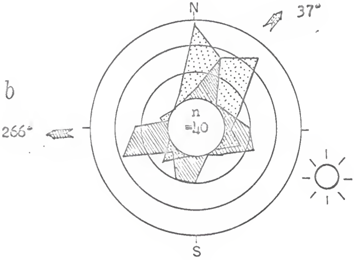
Fig. 24. Orientation of (a) *Menemerus bivittatus*, (b) *Phidippus regius*, and (c) *Plexippus paykulli* under the clear sky on June 27, 1966 and March 10, 1967. ░ controls, ▨ six hours phase-shifted.

a



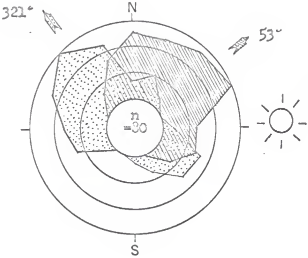
Menemerus bivittatus
March 10, 1967
0900-1000 EST

b



Phidippus regius
March 10, 1967
0900-1000 EST

c



Plexippus paykulli
June 27, 1966
0900-1000 EST

The Effect of Desiccation on the Light Reaction of *Plexippus paykulli*

Immediately after collection from the field, 50 adult spiders were briefly tested in the light-dark box. They showed a definite preference for the lighted side of the test chamber. A total of 180 spiders were desiccated for periods of four hours to ten days. Their subsequent behavior in the test chamber is expressed as excess percentage of their appearance on the illuminated side (Table 4).

TABLE 4. Effects of desiccation on the light reaction of *Plexippus paykulli*.

	Intensity of light reaction expressed as excess percentage on the illuminated side for each batch of five spiders	Mean
Without desiccation	+90, +24, +50, +42, +20	+48
	+82, +48, + 8, +80, +38	
Periods of desiccation:		
4 hours	+90, +72, +45, +10, -28	+38
8 hours	+80, +72, -40, -15, - 8	+18
12 hours	+30, + 8, -24, -32, -50	-14
24 hours	+64, +30, -50, -48, -10	- 3
2 days	+30, +10, -70, -60	-23
3 days	+40, +30, -70	0
4 days	+30, -80, -30	-27
5-7 days	+46, -64	-10
7-10 days	+92, +30, -20, -80	+ 3

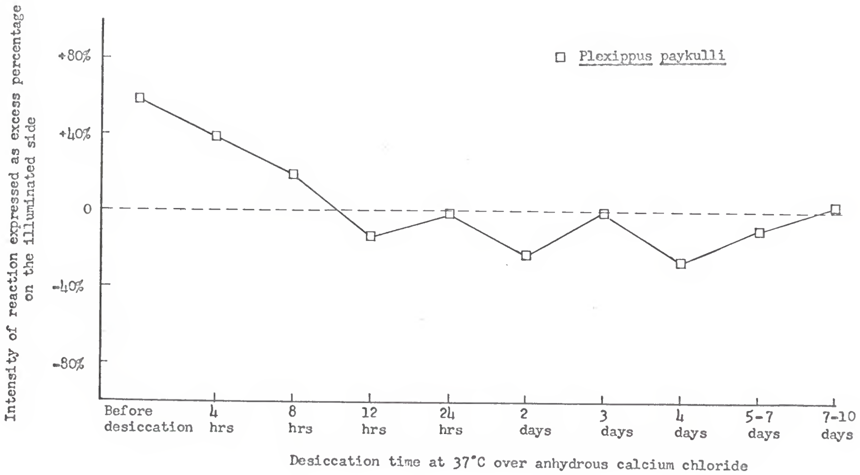


Fig. 25. Effect of desiccation on the light reaction of Plexippus paykulli.

The results of gradual desiccation indicate that the normally light-oriented spiders change to a preference for the dark (Fig. 25).

Oxygen Consumption and Acid Phosphatase Activity

The rate of oxygen consumption is expressed in microliters (μl) of dry gas (at 760 mm of mercury and zero degree centigrade) consumed per gram spider tissue (Fig. 26). The mean body weight of the spiders and a summary of the oxygen consumed during different parts of the day are exhibited in Table 5.

The relationship between body weight and rate of oxygen consumption is illustrated (Fig. 27a). This experiment reveals that more oxygen is consumed during the day than at night, and there is a marked difference in oxygen consumption between the first and the second half of the light period. In Menemerus bivittatus the oxygen consumption during the afternoon is about 37 percent higher than in the forenoon. In Plexippus paykulli it is about 23 percent higher, whereas in Phidippus regius the corresponding values are about equal.

In the experiment on acid phosphatase activity, the amount of P-nitrophenol produced is directly proportional to the amount of the enzyme acid phosphatase present in the tissues of the spider. The calculated values of P-nitrophenol per mg tissue of spider for the four categories are recorded in Table 6.

These results indicate that the adult females have about 74 percent higher values of acid phosphatase than the males. The penultimate stages of the two sexes show just the opposite condition, namely the males have about 100 percent higher values than the females of the corresponding stage (Fig. 27b).

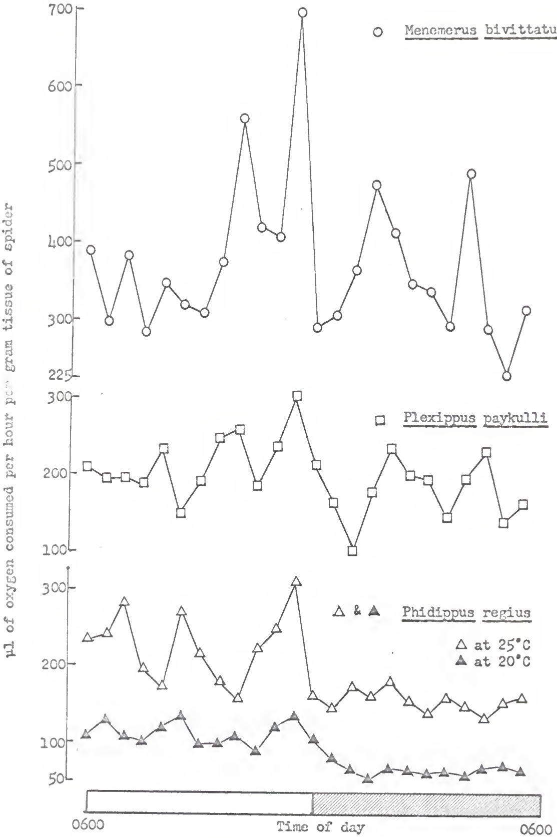


Fig. 26. Oxygen consumption in three species of jumping spiders at different times of the day.

TABLE 5. Body weight and oxygen consumption of the three species of jumping spiders.

	Menemerus bivittatus	Plexippus paykulli	Phidippus regius
Mean body weight:	0.0549 gms	0.1179 gms	0.8261 gms
µl of oxygen consumed per hour per gram tissue of spider			
1. For a 24 hour period	369	196	157
2. For 12 hour light period only	396	213	188
3. For 12 hour dark period only	341	178	126
4. For the first six hours of the light period	336	191	192
5. For the second half of the light period	461	236	185

TABLE 6. mM P-nitrophenol produced per mg tissue of Plexippus paykulli. Each value is the mean of four determinations.

		Male		Female
Adult		64.05x10^{-5} 29.89x10^{-5} 51.24x10^{-5} 25.42x10^{-5}		66.96x10^{-5} 85.56x10^{-5} 66.96x10^{-5} 70.78x10^{-5}
	Mean:	42.70x10^{-5}	Mean:	72.53x10^{-5}
Penultimate		53.50x10^{-5} 46.54x10^{-5} 37.45x10^{-5} 72.23x10^{-5}		15.78x10^{-5} 21.05x10^{-5} 21.85x10^{-5} 47.34x10^{-5}
	Mean:	52.45x10^{-5}	Mean:	26.30x10^{-5}

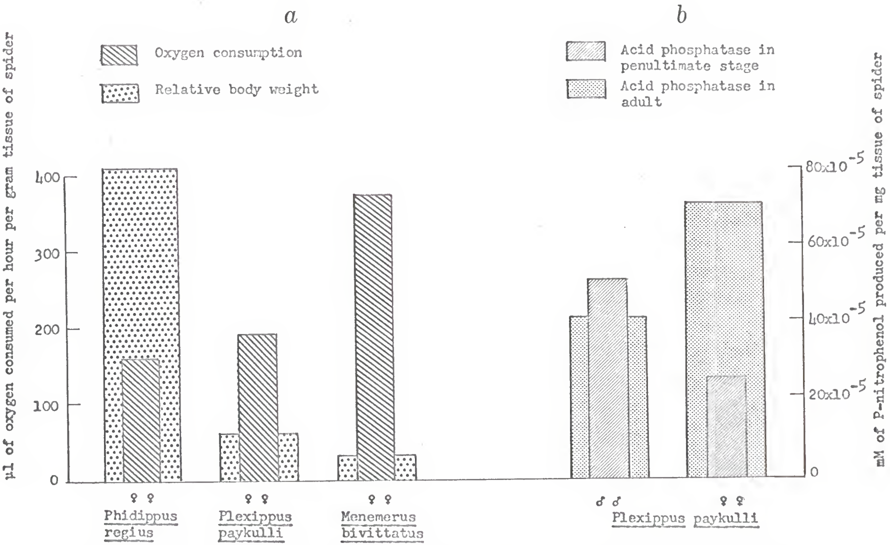


Fig. 27. (a) Rate of oxygen consumption in relation to body weight for the three species, (b) Acid phosphatase activity in adult and penultimate stages of *Plexippus paykulli*.

DISCUSSION

The behavior and activity cycles of salticid spiders have been poorly known to date. Among the few species studied, emphasis has been on the capture of prey, courtship and mating habits.

Activity Cycles

On the basis of their diurnal activities it has been assumed by most workers that jumping spiders are strictly diurnal. Field observations and laboratory recordings now show that the degree to which they restrict their activities to the daytime varies from species to species. Plexippus paykulli is more diurnal than Menemerus bivittatus and Phidippus regius. Crane (1949) noticed that the courtship patterns of different species reflect their evolutionary stage within the family. Field observations, made during the warmer months of the year, reveal that in nature the three species used in this study show two peaks of activity during the day; in the recordings in the laboratory the two peaks tend to merge. This parallels the behavior of Geotrupes described by Birukow (1960), where he attributed it to the influence of the light source which remained fixed in space during the whole experiment. Another reason for the merging of the two peaks can be the absence of rhythmic fluctuation of temperature under the experimental conditions.

For the three species light is an important 'Zeitgeber'; the onset of light initiates their activity. Under constant conditions the "free running" rhythm tends to shift gradually out of phase with the environmental cycle, as would be the case if the rhythm is endogenous; Halberg (1960) calls it "circadian." The experimental design did not permit an accurate evaluation of the free running period. A few statements may be made tentatively. In one individual of *Phidippus regius* the free running period is biased slightly above 24 hours, advancing in time in constant darkness. In the experiments the rhythm persisted under normal day-night and constant temperature conditions only for five to six days in the more primitive species *Menemerus bivittatus* and *Phidippus regius*; it became irregular after that, and the spiders became inactive. In *Plexippus paykulli* the rhythm persisted for ten to 15 days. The recordings also indicate that it reappeared when it did not show for a day or two. A temperature difference of ten degrees centigrade did not upset the rhythm of *Plexippus paykulli*. This species became increasingly active in continuous darkness. Under the same experimental conditions the periods remain the same or become slightly shorter in the other two species. Corbet (1960) generalized that diurnal animals when starved become more active at night. The fact that the spiders were not fed during the recordings is not taken into account; they are known to withstand starvation for long periods of time and, moreover, only the first four to six days of recordings were compared.

Orientation

The visual orientation of the three species was more consistent in direction (with a magnitude of their mean vectors above 0.7) during their periods of greatest activity than at other times of the day when they were relatively inactive in nature (magnitude below 0.7). Orientation experiments under the clear sky disclose that *Plexippus paykulli*, more than the other two species tends to remain oriented throughout the day. The magnitudes of the mean angles of the pooled data of each of the three species are so weak that no final conclusions can be drawn from these experiments. The orientation of *Plexippus paykulli* is similar to that of *Geotrupes* (Birukow, 1960). The angle of locomotion that *Plexippus paykulli* maintains to the sun decreases from sunrise to noon on its left side, and increases from noon on the right side, indicating a mechanism of time-compensated sun orientation. The other two species showed less reliable and predictable results, although a certain tendency to maintain individually preferred directions at different times of the day is evident.

Although many vertebrates and invertebrates use celestial bodies instead of local topographical features as reference points in their orientation (Santschi, 1911; von Frisch, 1950; Kramer, 1950; and Sauer, 1957, 1960), it is probable that most invertebrates use non-celestial mechanisms for establishing locations; such mechanisms may be superior and more effective for short distances (Birukow, 1960). The present findings indicate that these spiders, and in particular the more highly evolved *Plexippus paykulli*, have at least an ability of sun orientation intermediate between a menotaxis and an accurately time-compensated orientation. Experiments under the fixed light show that these spiders can maintain a certain angle to the light source, but they deviate to one side and the other at different times of the day. The experimental phase-shifts show that they are able to adjust to a new steady-state, and they are influenced in their directional choice by the phase difference.

The shift of their direction of orientation, however, is difficult to evaluate since no distinct pattern can be drawn from the experimental results. Further studies are needed.

Effects of Desiccation

The effect of desiccation on the light reaction of *Plexippus paykulli* indicated a gradual shift from a photopositive to a photonegative response during the first 24 hours of treatment. Afterwards the spiders showed very little light response and remained photonegatively oriented. This shift resembles that of *Drosophila* (Perttunen, 1963), and is the reverse of the condition exhibited by the normally photonegative arthropods *Calandra* and *Tenebrio* (Perttunen and Lahermaa, 1958). Pardi and Papi (1952) noted for the amphipod *Talitrus* that the amount of moisture affected their choice of escape direction. The adaptive value of this kind of response to desiccation is quite evident, and it may have its counterpart in the spiders' rest during the hot noon hours, which accounts for the biphasic nature of their activities.

Oxygen Consumption and Acid Phosphatase

Endogenous oscillations are the principal elements in many physiological time-measuring processes (Bünning, 1964). The rate of oxygen consumption parallels the cyclic pattern of activity of these spiders. The peaks of oxygen consumption correspond to the peaks of activity, although the spiders showed little activity during the test due to the limitations of the containers used. Comparison between the rate of oxygen consumption and the body weight for the three species shows that they are inversely proportional. This phenomenon has been found in small mammals (Prosser and Brown, 1961). Numerous studies of daily and seasonal fluctuation in various metabolites have been made in man and other animals, for example the rhythm of potassium excretion (Lobban, 1960), and the rhythmic fluctuation of blood sugar in the house cricket (Nowosielski, 1961). Estimates of the level of acid phosphatase activity in *Plexippus paykulli* show that the penultimate males have almost twice the amount of enzyme as the penultimate females. The high activity of enzyme probably correlates with the early onset of spermatogenesis. Since it was not possible to estimate the correct age of the adults it should be generalized with caution that adult females have more of this enzyme than adult males.

Locomotor, respiratory or enzymatic rhythms are processes under the control of the internal regulating mechanisms. As Bünning (1964) aptly put it, in all cases it is only the hand of the clock that has been investigated so far.

SUMMARY

Some aspects of the natural history of the three common jumping spiders *Menemerus bivittatus* (Marpissinae), *Phidippus regius* (Dendryphantinae) and *Plexippus paykulli* (Plexippinae) were studied in Gainesville, Florida. Specimens of the three species were used in experimental work for an analysis of their capacities of light orientation and recordings of some of their biorhythms.

While mostly diurnal, the more primitive forms *Menemerus bivittatus* and *Phidippus regius* also showed nocturnal activity under laboratory conditions, 19 and 29 percent of the total activity period respectively. Recordings under constant conditions revealed the endogenous nature of their activity cycles. *Plexippus paykulli* tends to increase its activity in continuous darkness. *Menemerus bivittatus* maintained about the same pattern of activity in continuous darkness as in light, while constant light made *Phidippus regius* continuously active. *Plexippus paykulli* was not influenced in its activity pattern when the temperature was raised from 25 to 35°C. Further, it adjusted gradually to a reverse rhythm of light-dark and reached a new steady-state within three days.

The individual spiders of the three species showed consistent orientation in various directions during their periods of greatest activity. At other times of the day, when they are relatively inactive in nature, they were not consistent in their directional choices. *Plexippus paykulli* displayed a pronounced tendency to keep the sun or an artificial light on one side during the first part of the day and on the other during the second half of the day. The other two species displayed the same tendency to a much lesser extent. Time-compensated sun orientation exists, but it appears not very well developed in the spiders studied. This is also indicated in their varying adjustments to phase-shifts.

Desiccations reverse the normal photopositive reaction of Plexippus paykulli and appears adaptively significant. The rate of oxygen consumption parallels the pattern of circadian rhythm as obtained by recordings of locomotor activities. Estimates of the level of activity of the enzyme acid phosphatase reveal it to be best developed in the penultimate males and mature females.

The investigations show that these jumping spiders are not exclusively diurnal in the laboratory. The establishment of a time-compensated sun orientation, although not correctly taking into account the hourly angular change of the sun, is evident as a species-specific development, more advanced in Plexippus paykulli than in the other two species.

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BIOGRAPHICAL SKETCH

George Jayasingh Phanuel was born on the 12th of January, 1927, at Madras, India. He graduated from the University of Madras with a B. Sc. degree with major in Zoology in 1948, and with an M. A. with major in Zoology in 1950. He was Lecturer in Zoology at the American College, Madura (1950-51). In 1951 he joined the faculty of the Madras Christian College. His work on the systematics of Madras spiders formed his thesis for a M. Sc. degree from the University of Madras in 1963.

An assistantship from the Department of Zoology at the University of Florida, together with a Fulbright Travel grant from the United States Educational Foundation in India, enabled him to work toward a doctoral degree from 1963-67. He is on leave from the Madras Christian College to which institution he will return after completion of his studies at the University of Florida.

He is married to Mirabai Pushpanathan Phanuel, and they have two sons.

This dissertation was prepared under the direction of the Chairman of the candidate's supervisory committee and has been approved by all members of that committee. It was submitted to the Dean of the College of Arts and Sciences and to the Graduate Council, and was approved as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

December 19, 1967

Dean, College of Arts and Sciences

Dean, Graduate School

Supervisory Committee:

Chairman

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December 19, 1967

E. Ruffin Jones

Dean, College of Arts and Sciences

Dean, Graduate School

Supervisory Committee:

Chairman